

THE HISTORICAL MISIDENTIFICATION OF
MARGARITIFERA AURICULARIA FOR *M. MARGARITIFERA*
(BIVALVIA, UNIONOIDEA) EXPLAINED BY THEIR ICONOGRAPHY

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ABSTRACT

Throughout its history, *Margaritifera auricularia* has been confused with its relative *M. margaritifera*. This paper compiles the early iconography of *M. auricularia* and reproduces the illustrations of this species. Our objective is to not only recapture the many interesting images of *M. auricularia*, but also to examine the historical errors that led to the confusion between the two species. After selecting valid representations of *M. auricularia* and its true synonyms, we see that this confusion has existed since Spengler (1793) first described the species. Indeed, we show that the first published image of *M. auricularia*, by Draparnaud (1805), was erroneously labeled as an image of *M. margaritifera*. We also reproduce several previously undiscovered illustrations of juvenile specimens of *M. auricularia*, as well as some interesting figures of *M. margaritifera* that were published before its description by Linnaeus (1758). One of these illustrations, Magnus (1555), is probably the first known image of a freshwater mussel.

FIRST DESCRIPTION OF *M. AURICULARIA*
AND ITS EARLY MISIDENTIFICATION WITH
M. MARGARITIFERA

The giant freshwater mussel, *Margaritifera auricularia*, is one of two European species of *Margaritifera*. Before its present rarity, it lived in the large, muddy rivers of western Europe and North Africa (Araujo & Ramos, 2000), whereas its relative *M. margaritifera* inhabited the smaller, colder rivers of northern Europe and North America. The characteristics of the fluvial habitat of *M. auricularia* have made it difficult to gather specimens. Thus, not only was this species discovered later, but it is less well known than *M. margaritifera*, which has been exploited since Roman times for its capacity to produce small pearls (Bonnemère, 1901).

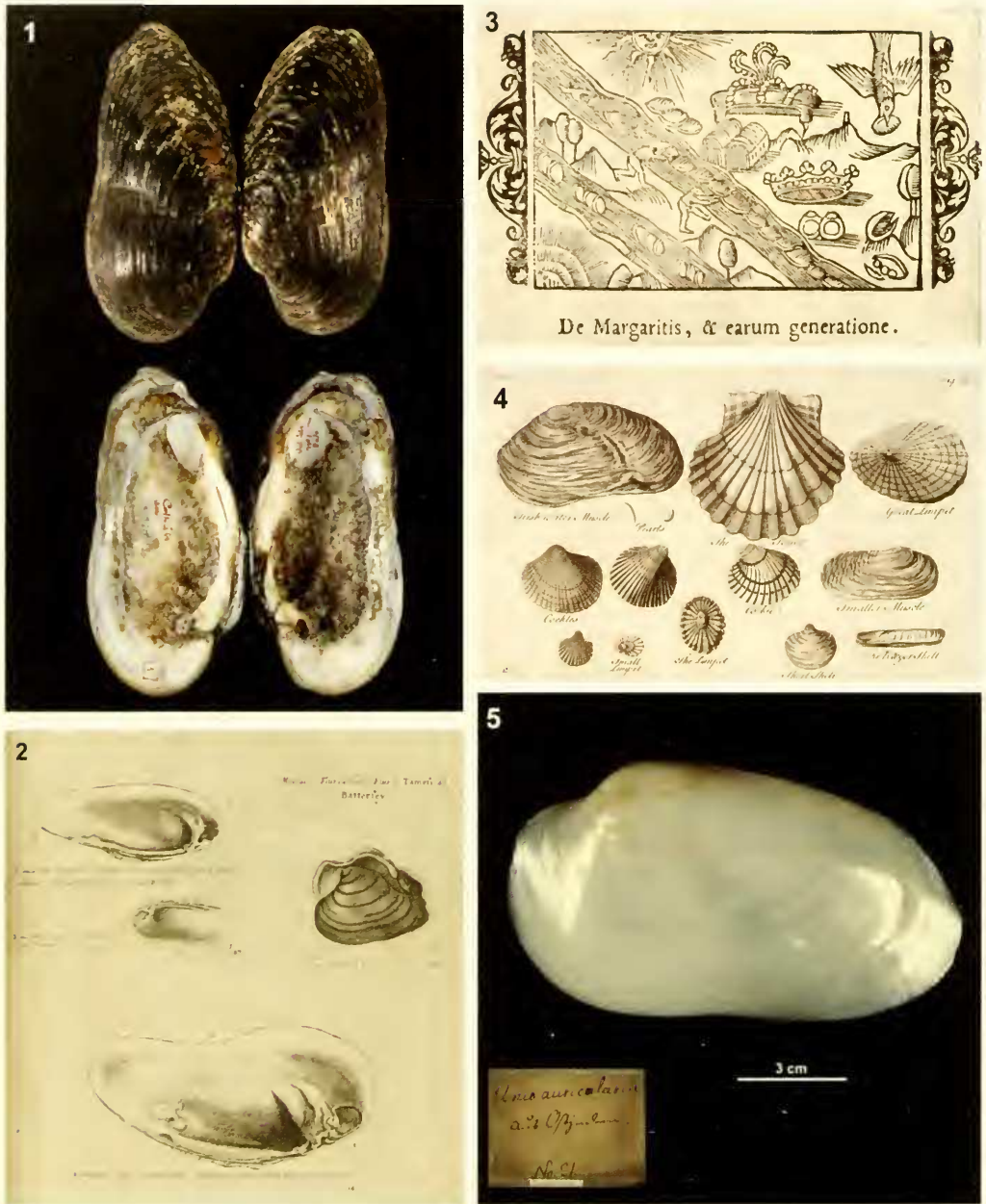
Margaritifera margaritifera was first described by Linnaeus (1758) as *Mya margaritifera*. *Margaritifera auricularia* was originally named as *Unio auricularius* by the Danish malacologist Lorentz Spengler (1793: 54–55), who erroneously cited the East Indies as its type locality. Although Spengler did not illustrate *U. auricularius*, his description of its large dorsal teeth and the hinge clearly differentiate it from *M. margaritifera*. Lamarck (1819)

described *Unio sinuata* (Fig. 1), which today is considered to be a synonym of *M. auricularia*.

Despite Spengler's description, both European species of the genus *Margaritifera* have been misidentified many times, and the first author to do so was, curiously enough, Spengler himself. In his original description, he cited a figure in by Martin Lister's *Historiae conchyliorum* (1686: fig. 149) as an illustration of *Unio auricularius*. However, Lister's figure shows the inside of a large, very sinuate *M. margaritifera* valve with pronounced cardinal teeth, and which at first glance resembles a valve of *M. auricularia* (Fig. 2). To confirm this, we tried unsuccessfully to find this specimen. Lister used shells from several collections to illustrate his book, mainly from his collection and that of William Courten. According to Wilkins (1953), the Courten collection was acquired by Hans Sloane, and the Sloane collection later became the nucleus of the British Museum collection, now in The Natural History Museum. Nevertheless, this *M. margaritifera* valve is not among the shells in the Sloane collection that were illustrated by Lister (Wilkins, 1953). It is possible that this valve was part of the Lister collection that was first owned by the Ashmolean Museum, and which

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FIGS. 1-5. FIG. 1: One of the syntypes of *Unio sinuata* Lamarck (MHNG 1086/75). Inscriptions by Lamarck are found in the interior of the valves; FIG. 2: Lister (1686: sheet of "plates", each a separate woodcut) with several freshwater bivalves and one right valve of *M. margaritifera* in pl. 149 (bottom). By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 3: A fishery of *M. margaritifera* by Magnus (1555). By permission of the Biblioteca Nacional, Madrid, Spain; FIG. 4: The illustration of *M. margaritifera* (upper left corner) by Pontoppidan (1755). By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 5: Type specimen and original label of *M. auricularia* from the Spengler collection.

was later moved to the Oxford University Museum of Natural History. However, Dance (1986) reported that none of the shells attributed to the Lister collection were there.

Simpson (1900) attributed Lister's figure to *M. margaritifera*, and Haas (1909), one of the most important researchers on freshwater mussels, also discovered Spengler's error, realizing that the lateral teeth were absent. This also meant that *M. margaritifera* had been illustrated by Lister nearly a century prior to its description by Linnaeus. There were at least two other authors who illustrated *M. margaritifera* before Lister. The first of these was probably Olaus Magnus (1555), a Swedish geographer, archbishop of Upsala and author of *Historiae de gentibus septentrionalibus*. His illustration of a catch of *M. margaritifera* (Fig. 3) was the first rough image of this species and perhaps the first ever of a freshwater mussel. Pontoppidan (1755), a bishop of Bergen, also illustrated *M. margaritifera* in his *The natural history of Norway* (Fig. 4). (This same figure was probably in the original 1753 edition, but we have not had an opportunity to examine it.) Other pre-Linnean authors, including Rondelet (1555) and Boussuet (1558), illustrated specimens of such other freshwater mussels as *Anodonta*.

Haas (1913) confirmed true identity of *Unio auricularius* in his paper on the *Unio* species described by Spengler. In an attempt to prevent future misidentification, he illustrated Spengler's polished specimen in the Natural History Museum of Copenhagen (Fig. 5).

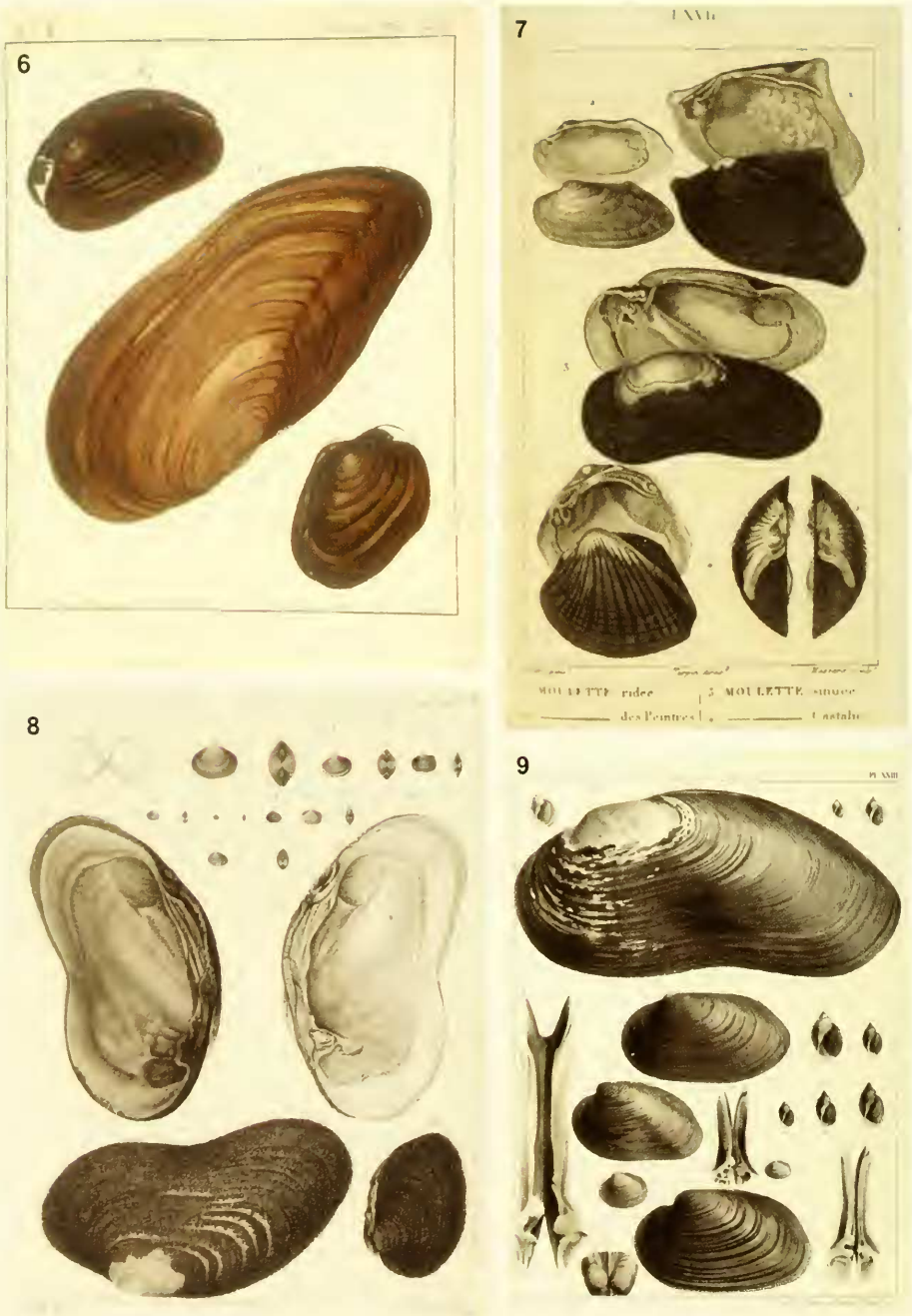
Several years prior to this, two European authors contributed to the confusion with their interpretation of freshwater mussel fossils discovered in Britain. Jackson & Kennard (1909) mistakenly attributed *M. auricularia* shells from Pleistocene sediments of the Thames River to *Unio (Margaritana) margaritifera* (Linnaeus) (= *M. margaritifera*). (*Margaritana* is an objective synonym of *Margaritifera*.) These authors noted the extraordinary size of the shells and concluded that "*Unio margaritifera* was living abundantly in the Thames". Haas (1910) and Jackson (1911) soon rectified this error when they confirmed that the fossils were actually *Unio sinuatus* (Lamarck) (= *M. auricularia*).

Just like their European counterparts, North American malacologists have also been confused by these *Margaritifera* species. For instance, Simpson (1900) used the names *Margaritana margaritifera* (Linnaeus) and

Margaritana crassa (Retzius, 1788) to refer to *M. auricularia*. Several years later, Kennard et al. (1925) suggested that this confusion was caused "partly through misidentification and partly because the later observers relied on the figures of their predecessors more than on their texts but chiefly because successive writers borrowed the synonymy of their fore-runners without checking it". Despite this observation, however, they also continued to make the same errors themselves. According to these authors, the *Mya margaritifera* from Schröter's *Die Geschichte der Flüsßconchylien* (1779: pl. 4, fig. 1) represents *M. auricularia* when, in fact, it is *M. margaritifera*. It is likely that they did not examine this figure, given that they considered their identification "unmistakable because of the strong lateral teeth and the peculiarities of the anterior muscular scars". These characters are absent in the above mentioned engraving, which clearly illustrates a specimen of *M. margaritifera*. After reading the authors' commentaries on another figure, we are certain that either they did not carefully study or did not understand Schröter's book. Schröter's specimen of *Mya testa crassa* is not, as they claim, a medium-sized specimen of *M. margaritifera*, but rather a normal specimen of *Unio crassus* (Fig. 6).

We see then that the confusion began with Spengler's erroneous interpretation of Lister's figure and was later complicated by the equally incorrect interpretation of *Mya testa crassa* (Schröter) by Kennard et al. (1925). Simpson (1900: 677, note 4) makes the same error by including *Mya testa crassa* (Schröter) as a synonym for the species *Margaritana crassa* (Retzius) in his records of *M. auricularia*. The confusion was perhaps caused by usage of the Latin *crassus* (meaning "very thick"), by both Lister, in his caption below the figure of *M. margaritifera (Musculus niger, omnium longe crassissimus, conchae longae species Gesn. Aldrov.)*, and by Spengler in his description of *Unio auricularius (Testa crassa, oblonga, etc.)*.

More interesting information is revealed about Lister's figure in his *Historiae animalium Angliae* (1681), some years prior to *Historiae conchyliorum* (1686). Here, Lister illustrates the same *M. margaritifera* valve that appears in the later work, along with valves from two other molluscs – *Unio pictorum* and *Anodonta* sp. The description of the *M. margaritifera* valve is only slightly different from that which appeared in *Historiae conchyliorum*: "Black



FIGS. 6-9. FIG. 6: Plate 2 of Schröter (1779). *Mya testa crassa* in fig. 2 (upper left corner) is actually *Unio crassus*. By permission of the British Library; FIG. 7: Blainville's (1827: pl. 67, fig. 3) figure of *M. auricularia* (middle). By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 8: Plate 10 of Draparnaud (1805). This is the first known illustration of *M. auricularia* (middle and bottom left). By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 9: Plate 23 by Dupuy (1851) representing one adult specimen (top) and the first known figure of a *M. auricularia* juvenile (middle) in figs. 7a and 7c, respectively. Fig. 7b (left) depicts the hinge of the adult. By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain.

mussel, entire shell very thick and very strong, from long shelled species after Gesner and Aldrovandi" [*Musculus niger, omnium crassissima et ponderosissima testa, conchae longae species Gesn. Aldrov.*]. However, further information written below the figure plainly pertains to *M. margaritifera*. For instance, Lister says: "It is sometimes fished with net in the deep whirlpools of the Tees River in Yorkshire, not so far from Dinsdale" [*In profundis voraginibus Fluvii Tees agri Eboracensis, non longe a Dinsdale, rete aliquando expiscatur*]. We know today that only *M. margaritifera* lives in Yorkshire Rivers.

ICONOGRAPHY OF
MARGARITIFERA AURICULARIA

We have reviewed all the early books on shells and malacology listed by Caprotti (1994) and Barbero (1999) (Table 1), as well as Simpson's (1900) list of synonyms for *Margaritana margaritifera* and *M. crassa*. Having confirmed that *Mya testa crassa* (Schroter) did not correspond to *M. auricularia*, the next author on Simpson's list to illustrate the species was Blainville (1827: pl. 67, fig. 3). In a lithography showing naiads (Fig. 7), Blainville identified the giant freshwater pearl mussel as *Unio sinuata* (or moulette sinuée). Nevertheless, Azpeitia (1933) discovered that another author, Draparnaud (1805), illustrated *M. auricularia* several years prior in his *Histoire*

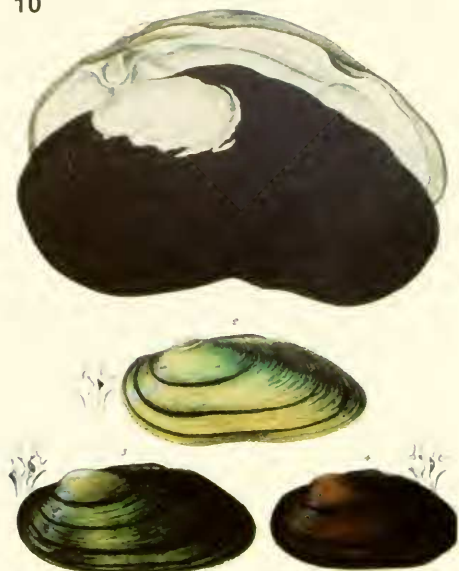
naturelle des mollusques terrestres et fluviatiles de la France (Fig. 8). This image went unnoticed because Draparnaud mis-identified both species of *Margaritifera* and labeled his image *Unio margaritifera*, Moulette margaritifera, or Moule du Rhin, although its real identity can be proven by the hinge teeth. Locard (1895) also reported this mistake in his *Étude sur la collection conchyliologique de Draparnaud*: "Draparnaud has made an error in respect of this species. His *Unio margaritifera*, cited by him as *Mya margaritifera* after Linné and Müller, really is the *Unio sinuatus* of Lamarck. We have specimens proceeding from the Loire River which are exactly similar to the one figured by him."

The next authors on Simpson's list to illustrate *M. auricularia* were Dupuy (1851) (Fig. 9), who drew the first known figure of a juvenile *M. auricularia*, Küster (1855) (Fig. 10), Rossmässler (1855) (Fig. 11), Moquin-Tandon (1855) (Fig. 12), Drouet (1857) (Fig. 13), G. B. Sowerby II (1868) (Fig. 14), and Locard (1893) (Fig. 15). Simpson also makes reference to: Bruguière (1797: pl. 248) [as "Deshayes, 1827"], Pfeiffer (1821), Rossmässler (1836, 1838, 1856), and Hanley (1856), but with the exception of Rossmässler (1856), the figures of these authors do not depict *M. auricularia*. Simpson (1900) wrote that the alleged *M. auricularia* specimens illustrated by Bruguière (1797) "look something like a heavy inflated *Lampsilis alatus* Say" [now *Potamilus alatus* (Say, 1817)]. In any event, the figured outline

TABLE 1. Historical illustrations of *M. auricularia*.

Author	Date	Figure(s)	Cited as
Draparnaud	1805	pl. 10, fig. 19	<i>Unio margaritifera</i>
Blainville	1827	pl. 67, fig. 3	<i>Unio sinuata</i>
Dupuy	1851	pl. 23, fig. 7a-c	<i>Unio sinuatus</i>
Küster	1855	pl. 37, fig. 1	<i>Unio sinuatus</i>
Rossmässler	1855	pl. 70, fig. 853	<i>Unio sinuatus</i>
Moquin-Tandon	1855	pl. 48, fig. 1	<i>Unio sinuatus</i>
Drouet	1857	pl. 2	<i>Unio sinuatus</i>
Sowerby	1868	pl. 62, fig. 311	<i>Unio sinuatus</i>
Locard	1893	figs. 163, 164	<i>Unio margaritanopsis</i> & <i>U. sinuatus</i>
Haas	1913	fig. 1	<i>Unio auricularius</i>
Haas	1916	fig. 1	<i>Margaritana auricularia</i>
Kennard et al.	1925	pl. 21, figs. 1-3	<i>Margaritana auricularia</i>
Haas	1929	figs. 181, 182	<i>Margaritifera auricularia</i>
Germain	1930	pl. 26, fig. 609, 615	<i>Margaritana auricularia</i> & <i>M.? margaritanopsis</i>
Azpeitia	1933	pl. 12, figs. 65, 66; pl. 13, fig. 67	<i>Margaritana auricularia</i>
Huckriede & Berdau	1970	pl. 1	<i>Margaritifera auricularia</i>
Fechter & Falkner	1990	color photo, p. 255	<i>Pseudunio auricularius</i>
Falkner	1994	photo, fig. 1	<i>Pseudunio auricularius</i>

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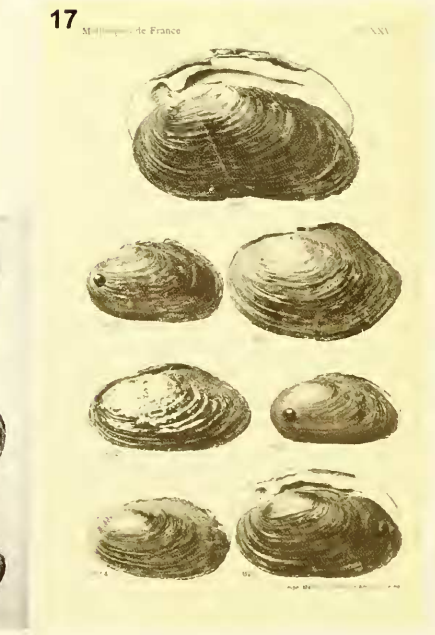
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FIGS. 10–13. FIG. 10: Plate 37 of Küster (1848). Top, *M. auricularia*; FIG. 11: Plate 70 by Rossmässler (1835) showing the hinge and a left valve of *M. auricularia*. By permission of the Österreichische Nationalbibliothek; FIG. 12: Plate 48 of Moquin-Tandon (1855). Fig. 1 (top) is *M. auricularia*. By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 13: Figure of *M. auricularia* in plate 2 by Drouet (1857). By permission of the Natural History Museum Picture Library.



FIGS. 14–18. FIG. 14: Plate 62 by G. B. Sowerby II (1868). Fig. 311 (middle) is *M. auricularia*. By permission of the British Library; FIG. 15: Page 151 of Locard (1893) showing a juvenile (top) and an adult specimen of *M. auricularia* (figs. 163 and 164, respectively). By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 16: The juvenile specimen of *M. auricularia* figured by Haas (1916). By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 17: Plate 26 of Germain (1930). Figs. 609 (top) and 615 (bottom right corner) depict an adult and a juvenile specimen of *M. auricularia*. By permission of the Museo Nacional de Ciencias Naturales, Madrid, Spain; FIG. 18a: *M. auricularia* in Azpeitia (1933: pl. 12); FIG. 18b: Adult (middle) and juvenile (bottom) specimens of *M. auricularia* in Azpeitia (1933: pl. 13).

of the shell and the presence of two siphons are characters that are completely absent in margaritiferids. The image by Pfeiffer (1821) is, in fact, *Potomida littoralis* (Lamarck, 1801), and it is the same species that Rossmässler (1836: pl. 13, fig. 195) drew and labeled *Unio sinuatus*. Rossmässler's (1838: pl. 35, fig. 493) figure of *Unio gargottae* Philippi, 1836, actually depicts *M. margaritifera*, and Rossmässler's (1856: pl. 80, fig. 853) is the same *M. auricularia* he illustrated in 1855. Lastly, the shell illustrated by Hanley (1856) identified as *Unio crassissimus* Hanley, 1843, another synonym of *M. auricularia*, may or may not be *M. auricularia*, as it is one of 60 very small illustrations of freshwater mussels on the same plate. It is interesting to note that *Unio margaritanopsis* Locard, 1893 (Fig. 15), is really a juvenile *M. auricularia*. Haas (1913, 1916, 1929) (Fig. 16), Kennard et al. (1925), Germain (1930) (Fig. 17), and Azpeitia (1933) (Fig. 18a, b) are the last historical authors to figure the species. Curiously, three of these four authors illustrated juvenile specimens. Haas (1916) and Azpeitia (1933) did so intentionally, but Germain assigns this juvenile as the type for a different species – *Margaritana margaritanopsis* (Locard), from the locality of Aiguillon, Lot et Garonne, the same locality of Locard's synonymous *Unio margaritanopsis*. The first of the figures by Haas (1913) depicts the polished type specimen from the Spengler collection, whereas the second (Haas, 1929) was reproduced from the figure by Dupuy (1851).

Some fossil valves were figured by Huckriede & Berdau (1970), but a new illustration of Recent *M. auricularia* did not appear until almost 60 years after the image by Azpeitia (1933), a color photo in Fechter & Falkner's (1990) guide to European land and freshwater molluscs. Several years later, Falkner (1994) photographed Spengler's type specimen of *M. auricularia* and designated it as the lectotype of the species *Pseudunio auricularius*. (*Margaritifera auricularia* is the type species of *Pseudunio* Haas, 1910, a subgenus sometimes used for it.) Since the rediscovery of *M. auricularia* in Spain, and after almost 60 years without records, many new illustrations have depicted this endangered species in all stages of its development (Araujo et al., 2002), illustrations that are very different from the earlier, yet charming lithographies and hand-colored engravings.

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